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ON THE WATER-CONDUCTING SYSTEMS OF SOME DESERT PLANTS.*

W. A. CANNON.

(WITH TEN FIGURES)

A STATEMENT by VOLKENS[1] to the effect that the ducts of the stems of the shrubs and trees of the Egyptian-Arabian deserts are relatively poorly developed led to an examination of these elements in the shrubs and trees which are growing within reach of the Desert Botanical Laboratory. It appeared at once that our native plants are not poor in water-conducting tissue; on the contrary they are very well provided for in this regard, and I cast about for some means of expressing this condition of affairs from a comparative standpoint. It was especially desired to compare these plants with those of the deserts of Egypt and Arabia, but since the direct comparison was impracticable, because VOLKENS does not give exact data, I have sought a way out of the difficulty by using irrigated desert plants of the species studied as controls. I assume that the desert plants if provided with an abundance of water are for practical purposes mesophytes, and if VOLKENS had in mind the plants of middle Europe, which might well have been the case, we have in this roundabout manner a means of instituting the desired comparison. Aside from this, the great difference in the development of the conductive tissue between desert forms that have been irrigated and those that have not is of considerable interest in itself.

THE PLANTS STUDIED.

This study includes as many of the native desert trees and shrubs as are readily obtained, and also such as have been irrigated in various places in whatever manner or degree. These are the hackberry (*Celtis pallida*), the creosote bush (*Covillea tridentata*), the candle bush or ocotillo (*Fouquieria splendens*), and a relative of the crucifixion thorn (*Zizyphus lycioides*), representing the shrubs; and the cat claw (*Acacia Greggii*), the mesquite (*Prosopis velutina*), and two species of palo verde (*Parkinsonia microphylla* and *P. Torreyana*), representing the trees.

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*Papers from the Desert Botanical Laboratory of the Carnegie Institution. No. 12.

[1] VOLKENS, G., Flora der ägyptisch-arabischen Wüste, p. 82.

These plants grow in habitats which are very unlike in appearance, and which presumably are dissimilar also in such fundamentals as soil characteristics and water supply. Speaking now of the vicinity of the Laboratory only, for a radius of about ten miles the habitats may be classed as (1) mesa, (2) river bottoms, (3) the rocky slopes of the lower mountains, and (4) the "draws" of these mountains. As regards the amount of water in the soil available to the plants, the river bottoms should be classed first, after which should be placed the draws; the rocky slopes and the mesa are frequently very dry. The mesa is peculiarly desertic, because a subsoil, the so-called "calliche," which is practically impervious to water, reaches within a few inches of the surface of the ground. The top soil, the adobe, is a clay. In the river bottoms the top soil is several feet in depth.

The mesquite and the cat claw are found especially on the bottom lands, where they may attain the size of forest trees, especially the former. Both of these trees adapt themselves to the drier habitats, however; but in such places they are of much smaller size and are gnarled and much changed in outward appearance. Celtis and Zizyphus also grow on the river bottoms; Fouquieria seems to be confined to the rocky slopes. *Parkinsonia microphylla* also is mostly found on rocky or well-drained slopes, while the other species of palo verde (*P. Torreyana*) is to be found in the draws at a lower level. Finally, the creosote bush, which is the characteristic shrub of the mesa, grows on the bottoms as well as on the mesa, and is there large and most vigorous. The natural distribution of these plants, and also the modification in form which they assume in the various habitats, point to the conclusion that the optimum conditions for them are attained where, other conditions being equal, water is to be had in abundance.[2]

That the greater vigor of the plants on the river bottom, as opposed to those on the mesa, for instance, is not due mainly, if at all, to differences in the character of the soil, is shown by the manner in which they react to an abundance of water when they are well irrigated, the substratum being otherwise the same. The creosote bush and both species of palo verde thrive equally well by the side of the same irrigating ditch, and the same is true of the other plants mentioned above. That is to say, each of these plants, whatever may be their natural habitat, is most vigorous where the water supply is adequate. The suggestion cannot be avoided, therefore, that the distribution of these plants in this vicinity is in some way indicative of their specific reaction to the minimum rather than to the optimum supply of water. The extent to which this phase of the reaction of desert plants to water may influence their present distribution in this vicinity will be the subject of future experimental investigation at the Laboratory.

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[2] Compare "The creosote bush (*Covillea tridentata*) in its relation to water supply," V. M. SPALDING, BOT. GAZETTE **38**:124. 1904.

As has been suggested above, the irrigated desert plants are the more vigorous in every way. The leaves are larger and are functional for a longer period, and the plants attain also much larger proportions than those that are not irrigated, and they also grow faster. To give but a single instance of the latter, a palo verde well-irrigated four years from the seed is now about eight feet high,while there are many of these trees in the neighborhood of the Laboratory, without doubt many times as old, that are not so high.

With the larger leaf surface of the irrigated plants one would look for a faster rate as well as for a larger total transpiration. Whatever may be the absolute transpiration of the irrigated forms, the structure of the stems of the irrigated as opposed to the non-irrigated plants indicates that the latter have the faster rate. That is, the non-irrigated stems have larger ducts and more of them per equivalent area of cross section than the irrigated stems, which can be taken as indicating the more rapid transpiration of the former.[3]

To anticipate the general conclusions to be drawn from this paper, we may therefore be justified in thinking that the desert plants of this locality, being probably better provided with conductive elements than those of the Egyptian-Arabian deserts, may also have a faster rate of transpiration.

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[3] PFEFFER, Physiology of plants 1: p. 216; HABERLANDT, Pflanzenanatomie 3d ed.), p. 288.

THE METHODS AND THE RESULTS.

The number of ducts of the woody cylinder was determined in the following manner and under the following conditions: The branches selected for study were as nearly of the same size as possible, namely 0.6^{cm} in diameter; it did not appear feasible to get them all of the same age. All of the sections were made midway between the nodes. In counting the ducts an arbitrary area as a standard of comparison was taken as follows. A circle 14^{cm} in diameter was drawn on metric paper and octants were struck off. By means of an Abbé camera lucida an image of the section was so thrown on the metric paper that the periphery of the woody cylinder and the two points delimiting any octant coincided. The standard octant had an area of $19.24^{sq\ cm}$ ($14^2 \times 0.7845 \div 8$). Since the magnification employed was 66 diameters, the area actually examined was $0.29^{sq\ cm}$, or $29^{sq\ mm}$.

The method of studying the ducts thus chosen gives the greatest prominence to the latest growth. This was desired for the reasons that the most active transfer of water probably takes place in the more peripheral ducts, and because I could be most sure of the recent history of the plants as regards irrigation.

The term "irrigated" as used in this paper needs a word of explanation. I have been obliged to take whatever plants I might find that had received any water in addition to the rains. In certain instances, to be detailed below, the plants were growing by the side of an irrigating ditch and without question had water in abundance every day of the year. In other cases they were a greater or less distance from the ditch; and in yet other instances the ditch was filled with water for a portion only of the time, say once a month, during the dry season. Some of the forms received little water artificially, as, for example, Zizyphus, which is in the cactus garden at the University of Arizona and is not irrigated oftener than once or twice in a year. When the plants received a small amount of water I have called them "semi-irrigated." The distinction between irrigated and semi-irrigated forms is thus purely arbitrary.

The accompanying table presents a summary of the study. The numbers refer to the number of ducts in $29^{sq\ mm}$ of stem cross section made under the conditions described above.

	Not irrigated	Irrigated	Semi-irrigated
Acacia Greggii	41	. .	23
Celtis pallida	51	42	. .
Covillea tridentata	80	20	. .
Fouquieria splendens	215	. .	85
Parkinsonia microphylla	19	19[4]	. .
Parkinsonia Torreyana	28	23[4]	. .
Prosopis velutina	51	25[4]	. .
Zizyphus lycioides	44	. .	39

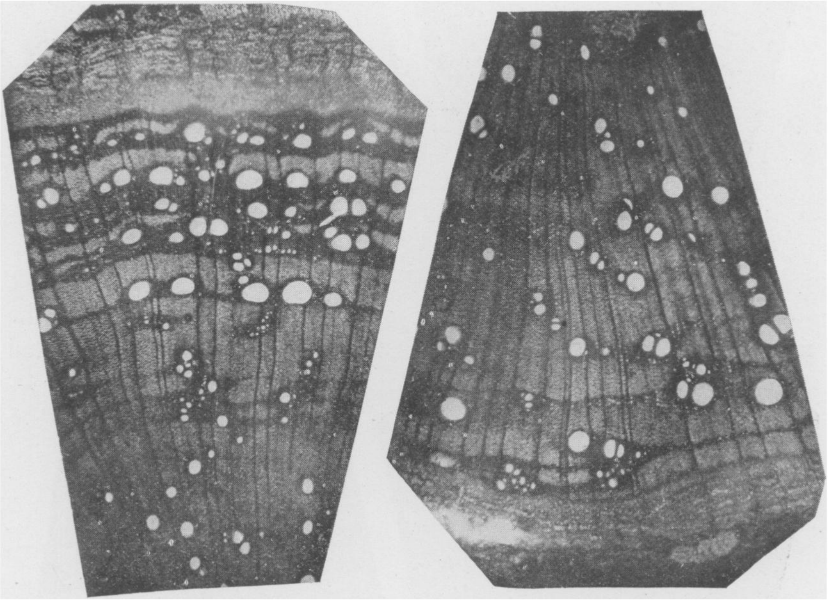

FIG. 1.—*Acacia Greggii:* left, not irrigated; right, irrigated.

The following outline indicates some of the conditions of growth of the plants studied.

ACACIA GREGGII (*fig. 1*).—The non-irrigated specimen was taken by the roadside between an old and at present unused irrigating ditch and the road ditch. Water stands in the latter for a considerable period after each heavy rain, and thus the effects of the rain are considerably prolonged. The irrigated form was growing about 6^m from a ditch in which the water flows the most or perhaps all of the year. The older portion of the non-irrigated stem does not

[4] The ducts of the irrigated plants were very small; see *figs. 5, 6, 7.*

have as many ducts as the more recent, an indication according to the present view that this plant might formerly have been irrigated. The owner of the field in which the non-irrigated specimen is found tells me that such, indeed, is the case.

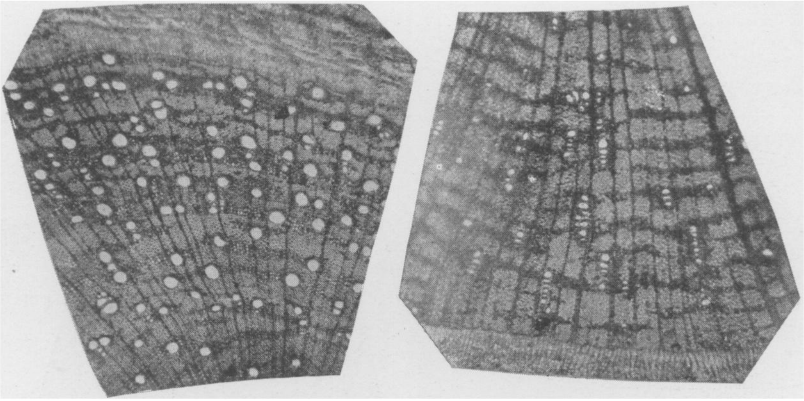

FIG. 2.—*Celtis pallida:* left, not irrigated; right, irrigated.

CELTIS PALLIDA (*fig. 2*).—The non-irrigated plant grows on the mountain on which the Desert Laboratory is situated. The irrigated plant is on the grounds of the University of Arizona, and has been watered occasionally.

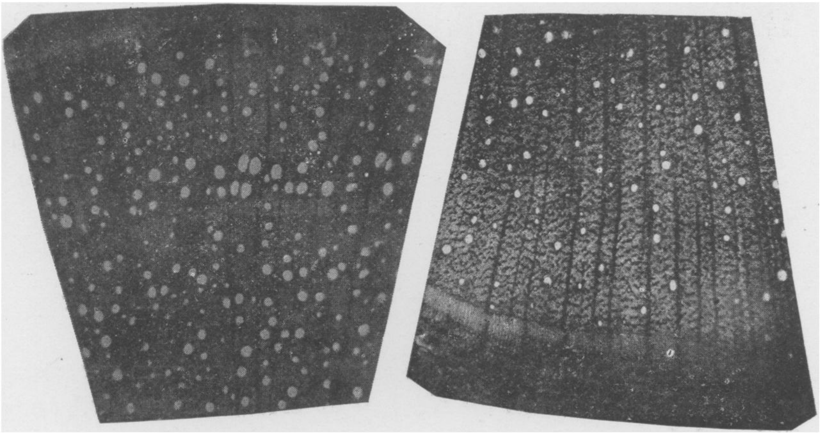

FIG. 3.—*Covillea tridentata:* left, not irrigated; right, irrigated.

COVILLEA TRIDENTATA (*fig. 3*).—The non-irrigated plant is on the mesa at the northern base of the laboratory mountain. The irrigated plant is growing by an irrigating ditch. Its roots are without question in a soil which is saturated with water all of the year. A third specimen, not figured, was originally chosen for study as being representative of the irrigated form. It was placed near an irrigating station and was supposed, therefore, to have received considerable water. When I examined the conductive system of this plant I found it to be essentially the same as the non-irrigated specimen. It was learned on inquiry that the plant had not been irrigated at all, a curious confirmation of the view advanced in this paper.

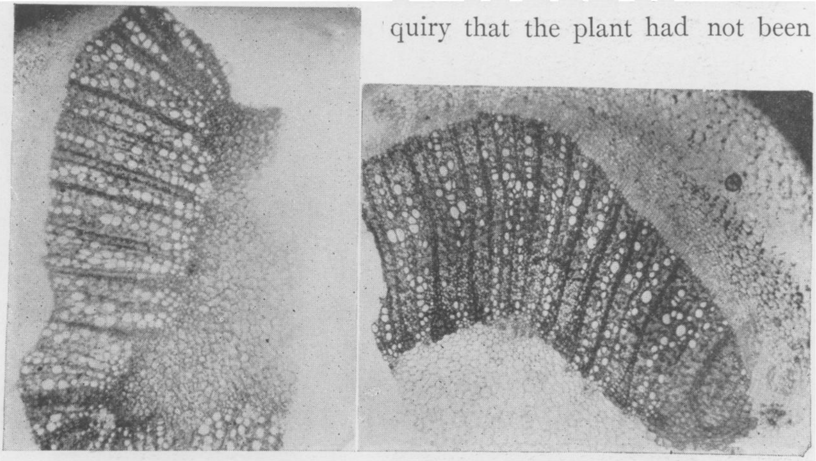

FIG. 4.—*Fouquieria splendens:* left, not irrigated; right, irrigated.

FOUQUIERIA SPLENDENS (*fig. 4*).—The non-irrigated specimen is growing on the mountain near the Laboratory. The irrigated is on the grounds of the Indian Industrial School, Tucson. It has received a variable amount of water, more during the past two years than formerly.

PARKINSONIA MICROPHYLLA (*fig. 5*).—The plant that is not irrigated is on the mesa at the northern base of the Laboratory mountain. The irrigated specimen is on the campus of the University of Arizona and has been irrigated frequently.

PARKINSONIA TORREYANA (*fig. 6*).—The non-irrigated palo verde is in the draw at the western base of the Laboratory mountain.

The irrigated plant is on the campus of the University of Arizona and has been irrigated in the same manner as the other species of palo verde given above.

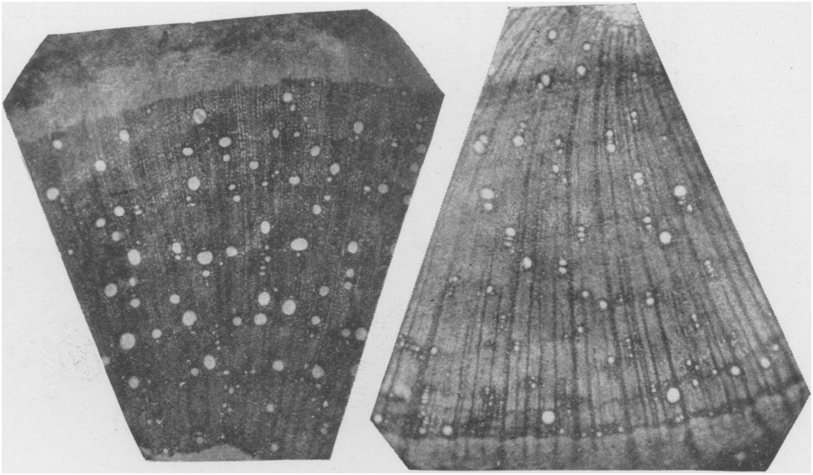

FIG. 5.—*Parkinsonia microphylla:* left, not irrigated; right, irrigated.

PROSOPIS VELUTINA (*fig. 7*).—The non-irrigated specimen of mesquite is growing near the Laboratory. It is about 2^m high, gnarled, and evidently in need of a better supply of water. The irrigated form of mesquite is growing near an irrigating ditch in

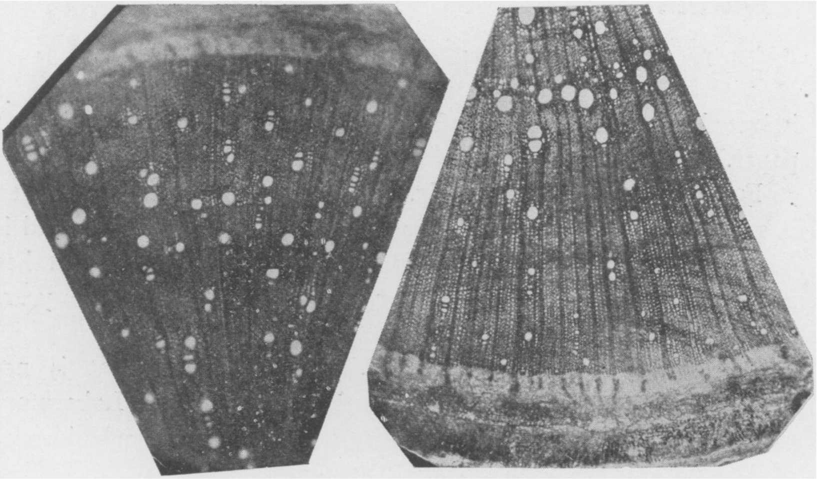

FIG. 6.—*Parkinsonia Torreyana:* left, not irrigated; right, irrigated.

which there is water several times during the year; not continuously as in the other ditch mentioned above.

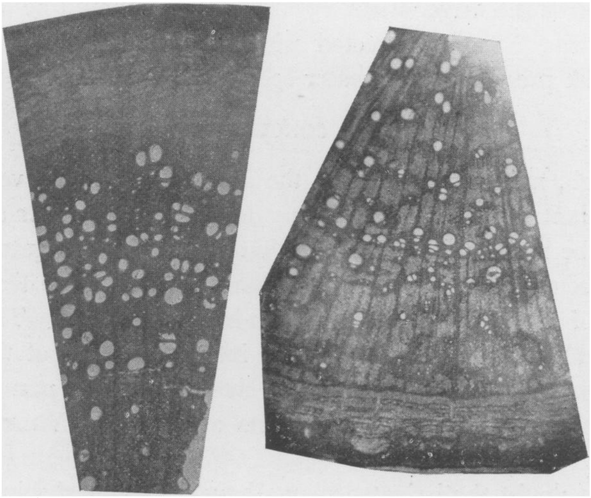

FIG. 7.—*Prosopis velutina:* left, not irrigated; right, irrigated.

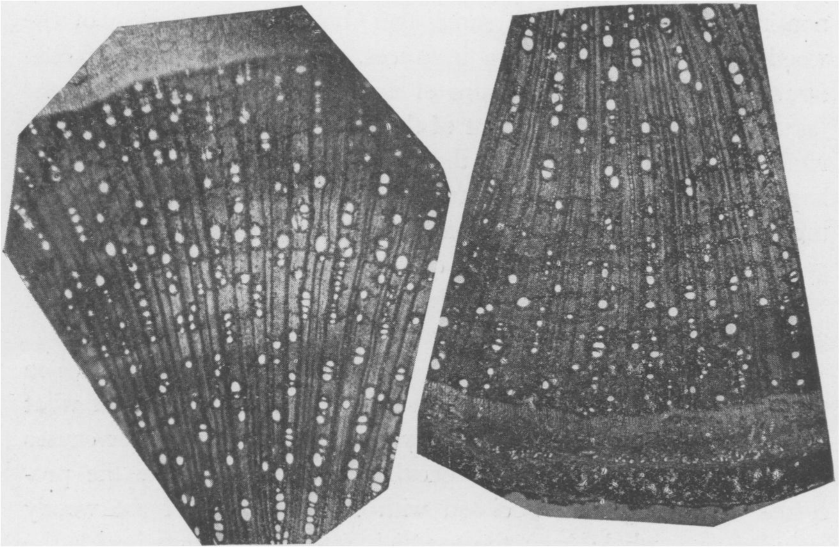

FIG. 8.—*Zizyphus lycioides:* left, not irrigated; right, irrigated.

ZIZYPHUS LYCIOIDES (*fig. 8*).—The non-irrigated plant is on the mesa near Tucson. The irrigated plant is growing on the campus of the University of Arizona in the cactus plantation. It receives water by direct application about twice a year. The nearest irrigating ditch is across the drive, about 13^m distant. It should be explained that the drive is so constructed with reference to the underlying calliche that presumably no water seeps across.

GENERAL CONCLUSIONS.

Although, much to my regret, the amount of water given to the irrigated plants is not known with any degree of exactness in any case, there can be no mistaking the fact that branches of irrigated plants (even if "semi-irrigated" only) are poorer in conductive tissue than branches of the same diameter of non-irrigated plants. This is an unexpected condition and of especial interest in view of the small development of the water-conducting elements in the non-irrigated forms of the Egyptian-Arabian deserts as given by VOLKENS. It merits further investigation.

Without doubt the irrigated plants have a greater absolute transpiration and organize each year a larger amount of wood than the non-irrigated plants of the same age; but the composition of the wood is different in the two instances. The irrigated plants construct a relatively large amount of non-conductive tissue each year (as compared with the amount of the other wood elements formed), while the reverse is true of the non-irrigated plants. So that it happens, in stems of equal diameter but not of the same age, that the non-irrigated and older stems have more vessels than the irrigated and younger. One other characteristic of non-irrigated stems was also noted, namely, their ducts were usually or frequently of greater diameter.

We find, therefore, a quantitative and a qualitative difference in the structure of irrigated and non-irrigated stems, and from what has been stated it appears that any adequate account of the causes which induce these structural peculiarities must separate the processes which may be associated with the formation of the woody cylinder as a whole from those which may be connected with the organization of that part of the wood that is primarily to conduct water.

I shall not presume at present to offer any hypothesis to explain the phenomena noted. It seems, however, on the surface of things, that such explanation must take into consideration the differences in the length and the character of the growing season of the two classes of plants. The irrigated plants probably do not cease growing during any month of the year and are most active when the temperature is also the highest. The curve of the growth of these plants probably is very nearly parallel to that of the temperature for the year. The non-irrigated plants are subject to the peculiar climatic conditions of the desert. The summer is the season of the maximum temperature. At Tucson there are each year two rainy seasons: that of winter, January–February; and that of summer, July–August. The period of the greatest vegetative activity occurs at the time of the midsummer rains (it is not known how the winter rains affect the growth of these forms), and all growth ceases very soon after the rains are over. The curve of growth of the non-irrigated plants would be very similar, no doubt, to that for the yearly rainfall. *Fig. 9* expresses in a graphic manner the annual rainfall and temperature at Tucson. It may be taken also to indicate the rate of growth of the non-irrigated and the irrigated desert plants.

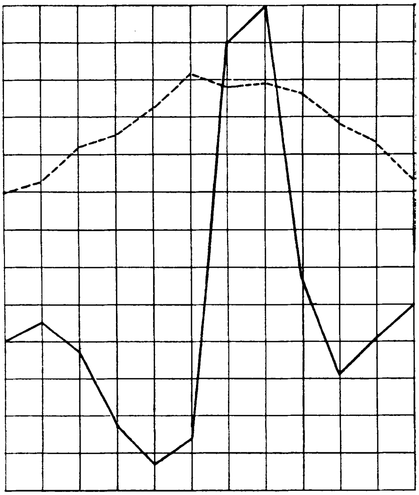

FIG. 9.—Mean yearly rainfall and maximum temperature at Tucson; broken line is temperature ($1^{cm} = 10°F.$); solid line is rainfall in inches ($1^{cm} = 0.2^{in}$).

Whatever may be the effect in detail, it must be admitted, I think, that the growth of the non-irrigated plants, and this may also be true of their transpiration, is directly associated with the distribution of the annual rains. Further, the intensity of this growth, as indicated by the structure of these plants and the general vegetal conditions of the desert, is probably directly connected with the fact that the heaviest rainfall occurs in summer. These facts encourage the view that the peculiar structure of the plants of the Egyptian-Arabian deserts, as regards the points under consideration, may likewise be due wholly or in part to analogous causes.

The climate of these foreign deserts is quite different from that of the desert about Tucson in the distribution, as well as the amount, of the annual rainfall; and consequently in the relation of the rainfall to the period of the highest temperature. The most rain occurs in the deserts of northwestern Africa and southwestern Asia in winter, but the maximum temperature is in summer.

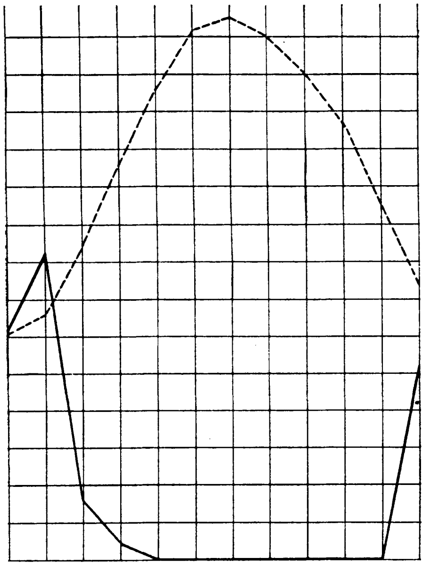

FIG. 10.—Rainfall and temperature at Cairo, Egypt, in 1887; broken line is temperature ($1^{cm} = 2^{\circ}C.$); solid line is rainfall ($1^{cm} = 1^{mm}$).

The period of the greatest vegetative activity in these deserts is in winter; in summer the plants are dormant. In the Egyptian-Arabian deserts, therefore, the renewal of growth occurs at the time of the year when the rainfall is also greatest, but not at the season of the highest temperatures. The curve of growth of the plants of this region probably coincides very accurately with the curve of the yearly rainfall. I have no means at hand of telling whether, on the other hand, if such plants were irrigated the period of their greatest growth would fall in summer. Such is apparently the case with some of the cultivated forms[5] in deserts farther west.

Fig. 10 represents the relation of the yearly rainfall to the temperature at Cairo, for the year 1887.

[5] SWINGLE, W. T., The date palm. U. S. Dept. Agric. 1904.

DESERT BOTANICAL LABORATORY.